Advances of study on atmospheric methane oxidation (consumption) in forest soil

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Abstract: Next to CO_2, methane (CH_4) is the second important contributor to global warming in the atmosphere and global atmospheric CH_4 budget depends on both CH_4 sources and sinks. Unsaturated soil is known as a unique sink for atmospheric CH_4 in terrestrial ecosystem. Many comparison studies proved that forest soil had the biggest capacity of oxidizing atmospheric CH_4 in various unsaturated soils. However, up to now, there is not an overall review in the aspect of atmospheric CH_4 oxidation (consumption) in forest soil. This paper analyzed advances of studies on the mechanism of atmospheric CH_4 oxidation, and related natural factors (Soil physical and chemical characters, temperature and moisture, ambient main greenhouse gases concentrations, tree species, and forest fire) and anthropogenic factors (forest clear-cutting and thinning, fertilization, exogenous aluminum salts and atmospheric deposition, adding biocides, and switch of forest land use) in forest soils. It was believed that CH_4 consumption rate by forest soil was limited by diffusion and sensitive to changes in water status and temperature of soil. CH_4 oxidation was also particularly sensitive to soil C/N, Ambient CO_2, CH_4 and N_2O concentrations, tree species and forest fire. In most cases, anthropogenic disturbances will decrease atmospheric CH_4 oxidation, thus resulting in the elevating of atmospheric CH_4. Finally, the author pointed out that our knowledge of atmospheric CH_4 oxidation (consumption) in forest soil was insufficient. In order to evaluate the contribution of forest soils to atmospheric CH_4 oxidation and the role of forest played in the process of global environmental change, and to forecast the trends of global warming exactly, more researchers need to studies further on CH_4 oxidation in various forest soils of different areas.

Keywords: Atmospheric methane; Oxidation; Global warming; Forest soil; Sink

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Introduction

Before the industrial revolution, the concentrations of greenhouse gases remained relatively constant in the atmosphere. Since then, they have increased in a large scale because of direct or indirect effects of human activities. Next to CO_2, methane (CH_4) is the second important greenhouse gas in the atmosphere, and its concentration has increased by about 150% (1.060 $\mu L \cdot L^{-1}$). Since 1750, it has increased by 1.760 $\mu L \cdot L^{-1}$ in troposphere currently, with an average increase rate of 0.007 $\mu L \cdot L^{-1} \cdot a^{-1}$. The direct radioactive forcing of 0.48 $W \cdot m^{-2}$ from CH_4 is 20% of the total from all of the long-lived and globally mixed greenhouse gases (IPCC 2001). The greenhouse warming potential of a molecule CH_4 is 21 times higher than that of CO_2 (IPCC 1992; Houghton et al. 1994). Therefore, with the time passed, the greenhouse effect of CH_4 will preponderate over that of CO_2, and it will raise the temperature of the earth surface further.

Based on the above-mentioned reasons, the global warming will be accelerated in speed in the coming years and bring more environmental problems for human society. In order to forecast this tendency exactly and find methods to control it, a large number of scientists have focused their research on aspects of atmospheric CH_4 sources and sinks.

The amount of CH_4 in the atmosphere should be a balance between CH_4 emissions (both natural and anthropogenic) and removal (Watson et al. 1990). The current emission amount from all sources (wetland, rice paddy, fossil fuel and biomass burning, landfills, ruminants, termites, ocean and so forth) is about 598 $Tg \cdot a^{-1}$. Based on reports in recent years, the global loss rate of atmospheric CH_4 is 576 $Tg \cdot a^{-1}$. Up to now, there are three sinks served as the role of removing atmospheric CH_4. The mean global loss rate of atmospheric CH_4 is dominated by its reaction with OH^- (506 $Tg \cdot a^{-1}$) in the troposphere. Other two approaches of CH_4 consumption are to transport to stratosphere (40 $Tg \cdot a^{-1}$) and to be oxidized in soil (30 $Tg \cdot a^{-1}$). Many studies suggested that atmospheric CH_4 may be oxidized (consumed) in various water-unsaturated soils (IPCC 2001) and forest soil has been proved having the biggest capacity in oxidizing atmospheric CH_4 (Boecks et al. 1998).

In the early days of twentieth century, it was known that bacteria could oxidize CH_4 (Munz 1915; Söhngen 1906). This knowledge was used widely in the field of petroleum

prospecting by taking CH_4 oxidizing bacteria as the sign of petroleum gases (Mogilevskii 1938, 1940). However, the concept of soil as a CH_4 sink was formed with an early report of CH_4 consumption in peat soils (Harriss *et al.* 1982). The uptake of CH_4 by forest soil was first reported by keller *et al.* (1983) in 1983, since then, CH_4 consumption in forest soils has been measured in many countries (Shigehiro *et al.* 2000; Nobuaki *et al.* 2003; Bradford *et al.* 2000; Brumme *et al.* 1999; Steinkamp *et al.* 2001; Whalen *et al.* 1992; Schnell *et al.* 1994; Billings *et al.* 2000; Phillips *et al.* 2001; Sun 2000; Dong *et al.* 2003; Prieme *et al.* 1996; Dobbie *et al.* 1996a; Prieme *et al.* 1999; Sitaula *et al.* 1995; Singh *et al.* 1997). The main knowledge of CH_4 oxidation (consumption) in forest soil is from the researches in Europe and USA. Nevertheless, up to now, there has not been an overall review in the aspect of atmospheric CH_4 oxidation in forest soil. This paper analyzed the main results in this field and provided some suggestion for further research.

Amount and rate of atmospheric CH_4 oxidation in forest soil

Forest soil is an important sink for atmospheric CH_4, but the contribution of CH_4 production, oxidation and transport to the overall CH_4 flux is difficult to quantify (Bradford *et al.* 2001). Although many studies showed that forest soil has the largest rate of uptake CH_4 in all kinds of CH_4 sink soils (e.g. arable soil, grassland soil, forest soil and tundra soil), (Willison *et al.* 1995; Dobbie *et al.* 1996a; Prieme and Chritensen 1999), so far there has not been reliable statistic estimation on the extent of atmospheric CH_4 oxidation in forest soil in literatures. The information in this field mainly derived from the researches in individual countries or districts.

The rate of atmospheric CH_4 oxidation in forest soil in Europe is estimated at about 0.6 $Tg \cdot a^{-1}$ (Dobbie *et al.* 1996b) and CH_4 uptake by temperate deciduous forests ranged from 0.5 $kg \cdot hm^{-2} \cdot a^{-1}$ to 5.5 $kg \cdot hm^{-2} \cdot a^{-1}$ (Keller *et al.* 1983; Steudler *et al.* 1989). In relatively undisturbed tropical ecosystems, CH_4 uptake in forests ranged from 0.5 $kg \cdot hm^{-2} \cdot a^{-1}$ to 2.5 $kg \cdot hm^{-2} \cdot a^{-1}$ (Keller *et al.* 1983; Keller *et al.* 1986; Seiler *et al.* 1984). Annual oxidation rates ranged from 0.1 $kg \cdot hm^{-2} \cdot a^{-1}$ to 2.5 $kg \cdot hm^{-2} \cdot a^{-1}$ under beech and spruce forest in Germany (Brumme *et al.* 1999).

A study conducted by Shigehiro *et al.* (2000) is worthy to mention. They measured the CH_4 flux in soils at seven sites in central Japan. Results showed that the soil CH_4 flux (3.8 $mg \cdot m^{-2} \cdot d^{-1}$) was nine times higher than the flux (0.42 $mg \cdot m^{-2} \cdot d^{-1}$) estimated by Dörr *et al.* (1992) in the medium soils. This suggested that the global CH_4 uptake rate might have been underestimated if it only depends on the data gained by Dörr *et al.* (1992). Therefore, more information from more regions of the world is needed to assess the current and future budget of atmospheric CH_4.

It is understood that the microbial activity depends on enzymatic processes and their environmental modulators.

Therefore, theoretically, any factors, which result in the change of CH_4 oxidizing microorgan..m communities and their activities whether inhibit or improve this process, will affect atmospheric CH_4 oxidation in forest soil. For the sake of expression, we generalize these influential factors into two types, natural and anthropogenic factors. The former includes soil physical and chemical characters, temperature, moisture, ambient greenhouse gases concentrations, tree species, fires and so on; the latter includes forest clear-cutting and thinning, fertilization, adding pesticides, exogenous aluminum salts and land use change. For a good understanding of these influential factors, studies on the mechanism and pathway of CH_4 oxidation in forest soil must be summarized first.

Mechanism and pathway of CH_4 oxidation

CH_4 oxidation process can be classified into atmospheric (exterior source) CH_4 oxidation and interior source CH_4 oxidation based on CH_4 coming from atmosphere or soils. According to this definition, CH_4 oxidation in forest soil belongs to the former. Species of methanotrophs participated in two types of CH_4 oxidation may be different due to different ambient CH_4 concentration. Many researches proved that CH_4 oxidation was abolished by autoclaving soil sample and atmospheric CH_4 oxidation in soil is a microbiological process (Bender *et al.* 1993), which need many CH_4 oxidizing bacteria and enzymes participating in. Besides methanotrophs, nitrifers and sulphate deoxidizing bacteria and methanogens may also oxidize little amount of atmospheric CH_4 (Bedar *et al.* 1989).

Methanotrophs

Methanotrophs are a subset of a physiological group of bacteria known as methylotrophs. Methanotrophs are unique in their ability to utilize CH_4 as a sole carbon and energy source, which are classified into six genera based on morphological difference, types of resting stages, the fine structures of intracytoplasmic membranes and some physiological characteristics (Whittenbury 1970, 1981, 1984). The known methanotrophs can be divided into three types: type I (*Methylosinas, Methylobacter, Methylococcus* and *Methylomicrobium*), type II (*Methylosinus* and *Methylocystis*) and type X (Hanson *et al.* 1996; Whittenbury *et al.* 1984), based on their morphology, physiology, phylogeny and the differences in pathways for CH_4 oxidation and formaldehyde assimilation and enzyme utilized (Hanson *et al.* 1996; Murrell *et al.* 1998). Type X was added to ac commodate methanotrophs similar to *Methylococcus capsulatus* that, like type I methanotrophs, utilize ribulose monophosphate (RuMP) as the primary intermediate for formaldehyde assimilation. Type X methanotrophs were distinguished from type I methanotrophs because they also possessed low levels of enzyme present in the Calvin-Benson cycle (Hanson *et al.* 1996; Whittenbury *et al.* 1984).

Pathways for CH₄ oxidation and formaldehyde assimilation

Using the enzymes known as CH_4 monooxygenases to catalyze the oxidation of CH_4 to methanol is a defining characteristic of methanotrophs. Fig. 1 illustrates the metabolism of substrates by methanotrophs; the common features include the central role of formaldehyde as an intermediate in catabolism and anabolism, and the unique pathway for the synthesis of intermedia in central metabolic routes (Hanson et al. 1996).
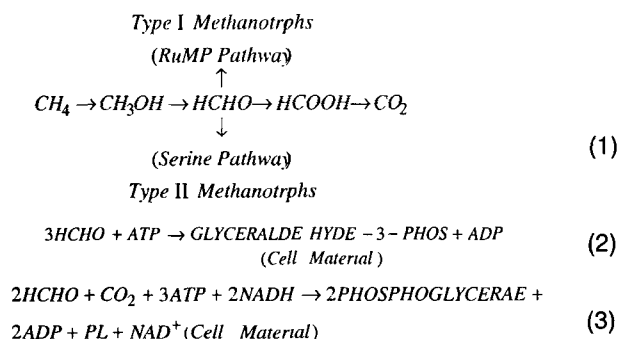
$Type\ I\ Methanotrphs$

$(RuMP\ Pathway)$

$\uparrow$

$CH_4 \rightarrow CH_3OH \rightarrow HCHO \rightarrow HCOOH \rightarrow CO_2$

$\downarrow$

$(Serine\ Pathway)$ (1)

$Type\ II\ Methanotrphs$

$$3HCHO + ATP \rightarrow GLYCERALDE\ HYDE - 3 - PHOS + ADP \atop (Cell\ Material)$$ (2)

$$2HCHO + CO_2 + 3ATP + 2NADH \rightarrow 2PHOSPHOGLYCERAE +$$

$$2ADP + PL + NAD^+ (Cell\ Material)$$ (3)

Fig. 1 Pathways for CH₄ oxidation and formaldehyde assimilation

(1) CH₄ oxidation pathways; (2) RuMP pathway; (3) Serine pathway

The microbiological metabolic process of atmospheric CH_4 oxidation in forest soil was measured by radiotracing techniques (Roslev et al. 1997). Results showed that the atmospheric CH_4 oxidized (31%-43%) were assimilated into microbial biomass; the residual CH_4 was recovered as $^{14}CO_2$. CH_4-derived carbon was incorporated into all major cell macromolecules by the soil microorganisms (50% as proteins, 19% as nucleic acids and polysaccharides, and 5% as lipids). Mancinelli (1995) believed that the most of C fixed in the process of CH_4 oxidation are transformed into microbial biomass other than CO_2.

CH_4 consumption by soils was stimulated by the addition of methanol (Benstead et al. 1998; Jensen et al. 1998). These results suggest that methanol or other non-methane substrates may promote atmospheric CH_4 oxidation in situ.

Kinetics of CH₄ oxidation

We know very little about the kinetics of the microbial CH_4 oxidation process, especially at low ambient concentrations. CH_4 oxidation rates in soil fluctuated with atmospheric CH_4 concentration, and this relationship may be described by the Michaelis-Menten equation (Equation (1)) (Bender et al. 1992, 1993; Dunfield et al. 1993):

$$V = \frac{V_{max}\ C}{K_m + C}$$ (1)

where V and V_{max} are CH_4 oxidation rate and its maximum rate, respectively; C is CH_4 concentration; K_m is the CH_4 concentration while oxidation rate reached half of the maximum, which is called half saturation constant. Bender

and Conrad (1993) investigated the kinetics of CH_4 oxidation in three different soils (forest soil included) under oxygenic conditions. Results showed that CH_4 oxidation followed a Michaelis-Menten kinetic with K_m of about (22 ± 35), $(\pm SE\%)$ $\mu L \cdot L^{-1}$ and V_{max} of about (3.60 ± 8) $nmol \cdot h^{-1} \cdot g^{-1}$ (dry weight soil).

Besides K_m and V_{max}, another kinetic parameter of CH_4 oxidation, which determines the ability of bacteria to grow on atmospheric CH_4, is threshold-mixing ratio (Th). Measured (Th_m) and approximated (Th_a) threshold mixing ratios for CH_4 oxidation are (0.02 ± 29) $\mu L \cdot L^{-1}$ and (2.72 ± 16) $\mu L \cdot L^{-1}$, respectively in forest soil (Bender et al. 1993). Two different CH_4 oxidation activities could be distinguished through biphasic saturation curves that CH_4-preincubated soils displayed. The first activity with a high affinity for CH_4 was comparable with the activity in fresh soil, and was adapted to low ambient CH_4 mixing ratios. This activity displayed low values for K_m, V_{max} and Th_a. A second activity with a low affinity for CH_4 appeared only after pre-incubation at increased CH_4 mixing ratios, and displayed high values for K_m, V_{max} and Th_a (Bender et al. 1992; Ridgwell et al. 1999).

Natural factors affecting atmospheric CH₄ oxidation in forest soil

Soil physical and chemical characters

The habitation of CH_4 oxidizing bacteria in forest soil mainly lies on the soil physical and chemical characters (e.g. gas diffusivity and air permeability, bulk density, soil acidity, soil carbon and nitrogen status). The primary factor controlling CH_4 oxidation rate in upland soil is the force of atmospheric CH_4 diffusing into soil (Born et al. 1990), which is highly dependent upon soil moisture content (Czepiel et al. 1995).

Ball et al. (1997) conducted an experiment in the laboratory and in situ. Results showed that there existed a positive relationship between atmospheric CH_4 oxidation rates and gas diffusivity, and air permeability in forest soil respectively. The reason is that the net transport of atmospheric gases into and out of soil systems is primarily controlled by diffusion along gas partial pressure gradients. Nevertheless, in general, the capacity of the methanotrophs consuming CH_4 commonly exceeds the potential of CH_4 diffusing from the atmosphere to the consumers. Therefore, it is understandable that the maximum rate of atmospheric CH_4 oxidation in forest soil is limited by diffusion, and can be calculated by parameters of soil physical properties and by the CH_4 concentration gradient. The contribution of CH_4 concentration along soil depths is theoretically described by the equation for gaseous diffusion with homogenous chemical reaction in porous unsaturated media. This allows for calculating the rate of CH_4 consumption in situ within specified depth intervals (Striegl 1993). Meanwhile, combined with the immediate inhibition of CH_4 uptake on waterlogging soils, findings also suggested that soil CH_4 diffu-

sion was an important regulator of CH_4 uptake (Bradford *et al.* 2001a).

In 2000, Smith *et al.* (2000) found a significant negative correlation between CH_4 oxidation and bulk density of soil. Rates of CH_4 oxidation are the highest in coarse-textured forest soil with well-developed soil structure and a permeable surface organic layer. Similar trends were expressed in other papers (MacDonald *et al.* 1996; Lessard *et al.* 1994). The reason was that compaction made soil lose macro-pores, which leaded to the reduction in gas diffusivity of soil.

Soil acidity is another major factor affecting atmospheric CH_4 oxidation in forest soils. Studies conducted in Germany showed that the soil with high acidity had a low CH_4 oxidation rate, compared to less acid soils, and suggested that the thickness of upper organic layer increased with increasing acidity, which did not contribute to CH_4 oxidation but acted as a diffusion barrier, especially when upper organic layer was wet. On the contrary, the CH_4 oxidation rate increased when this upper organic layer was removed or the mineral soil was homogenized by sieving. Obviously, the diffusion of atmospheric CH_4 is an important factor controlling oxidation in forest soils (Brumme *et al.* 1999). On the other hand, soil acidity may affect the activity of methanotrophs and pertinent enzymes. So from a biological point of view, there ought to exist an optimum range of soil acidity for CH_4 oxidation. Shen and Cao (1998) suggested that the optimum range of soil pH is from 6 to 7. But Sitaula *et al.* (1995) found that soil acidification (from pH=3 to pH=5.5) may result in a net increase in CH_4 uptake. The differences in research results may be due to the differences in other environmental factors.

Singh *et al.* (1997) present data to show that the long-term mean CH_4 uptake is governed by soil carbon and nitrogen status. At given soil moisture, net CH_4 uptake in a site rich in organic matter is lower than that in a site poor, the reason may be that organic matter-rich soil can easily become anoxic. However, a recent study indicated that CH_4 flux in the field was not correlated with water content, inorganic N content, or water-soluble organic carbon directly, but was correlated with soil C/N ratio (r =0.64, $p<0.001$), (Tamai *et al.* 2003).

Temperature and moisture

Oxidizing CH_4 bacteria are very tender. Low temperature and desiccation will diminish their activities. Their maximum biomasses are supported by the optimum soil moisture and temperature (Nesbit *et al.* 1992; Whalen *et al.* 1990). These points of view were proved by a number of studies. In 1997, Singh *et al.* (1997) measured the mean CH_4 uptake rates by soils of a seasonally dry tropical forest of India and believed that the seasonal variations were largely controlled by soil moisture. In summer, CH_4 uptake positively related to soil moisture, but in winter, the statuses were inversely. In their study, CH_4 consumption reached the highest value around soil moisture of 19%; thereafter it declined with

further increase in soil moisture, attaining the minimum value at soil moisture content of 18% in the rainy season. Czepiel *et al.* (1995) believed that the CH_4 oxidation rate maxims occurred at different moisture contents from 30% to 51% in each soil sample in wooded area. Some researchers suggested that the optimum soil moisture was related to soil organic matter content. Maximum oxidation rate often occurs in soil moisture content of approximately 33% and soil organic matter content of approximately 14%. Meanwhile, correlation analysis revealed that CH_4 oxidation rates were positively correlated with soil temperature and negatively with soil moisture ($p<0.001$), (Dobbie *et al.* 1996a). Moisture was the primary control factor in CH_4-sink soils of boreal forest soils, but at low soil temperatures (<10 °C), temperature was a stronger modulator (Whalen *et al.* 1996; Steinkamp *et al.* 2001a). They found that the optimum water content for CH_4 oxidizing is about 24%, and the CH_4 oxidation rate showed a modest decline with decreasing temperature over the entire range of WHC (water holding capacity) percentage, but a rapid decrease as soil moisture approached the highest values of WHC percentage. Water stress control of CH_4 oxidation must also be considered. Increasing the percentage of WHC from 13% to 25% resulted in a 22% increase in the CH_4 oxidation rate. In laboratory experiments, the gravimetric water content of 12% led to the maximum CH_4 oxidation. The CH_4 oxidation was still 60% of the maximum at water content of 4% and totally inhibited at water content of 1%. The results reveal that low soil water content is not an important factor in restricting CH_4 oxidation in mineral soil of boreal forests (Saari *et al.* 1998). Sitaula *et al.* (1995) suggested that the increased soil moisture from 32% to 42% (V/V) significantly reduced CH_4 uptake.

Sitaula *et al.* (1995) suggested that soil CH_4 oxidation could continue in the winter with temperatures near freezing point, CH_4 uptake rate ranged from 0.04 $mg \cdot m^{-2} \cdot d^{-1}$ to 0.4 $mg \cdot m^{-2} \cdot d^{-1}$ during the winter, which were 3%-22% of the maximum uptake rate observed in summer ($T>15°C$). Castro *et al.* (1993) believed that the CH_4 oxidation rate was positive correlated with soil temperature at -5°C -10 °C in spruce-fir forests soil. Dong *et al.* (1996) suggested the range of temperature is 0-30 °C. Experiments made in Beijing hilly area by Sun (2000) have demonstrated a similar result, the CH_4 oxidation rate was positive correlated with soil temperature at the depth of 5 cm. Forest soil surrounding the dam-lake always took up CH_4, even in the snow-covered soil. The CH_4 uptake rate increased as soil temperature increased. CH_4 uptake during the snow-covered season accounted for 18% of the annual uptake (Morishita *et al.* 1999). Optimal CH_4 consumption occurred in samples incubated at temperatures between 20 °C and 30°C and was greatly reduced at 40°C (Nesbit *et al.* 1992).

Ambient CO_2, CH_4 and N_2O concentrations

Many studies were conducted about effects of ambient

CO_2, CH_4 and N_2O on CH_4 consumption in forest soil. The net CH_4 consumption was significantly lower in forest soil under elevated CO_2, under similar conditions of moisture, temperature, NO_3^- and NH_4^+ concentrations. CH_4 consumption from May to October in elevated CO_2 soils was 47% less than that in ambient CO_2 soils (Phillips *et al.* 2001). Rigler and Boltenstern (1999) believed also that CO_2 at high concentrations had an inhibitory effect on CH_4 microbial uptake. Therefore, the contemporary increase in atmospheric CO_2 may negatively affect the soil CH_4-oxidizing community of upland forest soils and reduce the sink strength of these ecosystems in the atmospheric CH_4 budget. Contrary to CO_2, the actual contribution of soils as a CH_4 sink has increased, driven by increased CH_4 mixing ratios since industrialization (Willison *et al.* 1995). The calculations indicate that 54% of current CH_4 uptake by UK soils is the result of increased CH_4 mixing ratio.

There is a trade-off relationship between N_2O emission and CH_4 uptake, that is, the CH_4 uptake rate is increasing while the N_2O emission declined, the CH_4 uptake by forest soil began to fall while it increased. The relationship between N_2O emission and CH_4 uptake was not described as liner relationship but as a non-liner relationship, that is, there is a negative correlation ($P<0.01$) between $\log N_2O$ and $\log CH_4$ (Xu *et al.* 1995; 1999). Sitaula *et al.* (1995) also found a weak negative correlation between CH_4 uptake rate and N_2O fluxes ($r=-0.30$, $P<0.001$) and a significant negative correlation with soil N_2O concentration ($r=-0.57$, $P<0.0001$). The reason consists in the favorable conditions for N_2O production (nitration), such as high moisture content and restricted diffusion, are unfavorable for CH_4 oxidation.

Tree species

The average rate of the CH_4 uptake of coniferous forest soil was lower than that of deciduous forest soil (Shigehiro *et al.* 2000). Many studies have obtained similar results (Born *et al.* 1990; Castro *et al.* 1995; Dobbie *et al.* 1996b). The reason may be that the methanotroph was isolated from acid soil of coniferous forest. Xu *et al.* (1995) measured the CH_4 flux of various vegetations along an altitudinal gradient on the northern slope of Changbai Mountain. The results showed that mixed coniferous-deciduous forest soil have the largest amount of CH_4 uptake, followed by coniferous forest soil. Moreover, the amount of CH_4 uptake by the birch forest soil at high elevation is the smallest one. Moreover, some scientists believed the effects of trees of different species on CH_4 consumption realized by its influence to soil moisture (Menyailo *et al.* 2003).

Currently, there is no generally accepted theory concerning effects of tree species on CH_4 oxidation in forest soils, therefore, further research is needed.

Forest fire

The effect of forest fire on atmospheric CH_4 oxidation in forest soils has received only limited attention. On one hand,

forest fire kills soil microorganism by high temperature directly; on the other hand, it can result in the change of soil environment (Zhang *et al.* 2002), carbon and Nitrogen dynamics, and affect microbial process indirectly according to fire intensity and duration. Prieme and Christensen (1999) found that fire decreased CH_4 uptake. Soil water content at the burned site was somewhat higher than that at the unburned site (63% versus 54% of WHC), which may explain the difference in CH_4 uptake rate in some degree. Another researcher also reports that biomass burning had a small effect on CH_4 consumption by forest soil (Delmas *et al.* 1991). Meanwhile it is worth to point out that CH_4 emission amount is 167 $Tg \cdot a^{-1}$, about 44% of total CH_4 source is due to forest fires (Wang *et al.* 1998; Wang *et al* 2001; Levine *et al.* 1995). It is obviously that forest fire affects CH_4 oxidation in soils by the way of changing methanotrophic activity and soil physical and chemical characters. Nevertheless, we have no sufficient knowledge to assess the contribution of fire to atmospheric CH_4 budget.

In general, CH_4 consumption by forest soils appears diffusion limited (Czepiel *et al.* 1995), and is more sensitive to changes in soil water status than changes in temperature. CH_4 oxidation is also particularly sensitive to soil C/N, Ambient CO_2, CH_4 and N_2O concentration, tree species and fire in forest soils.

Anthropogenic factors influencing atmospheric CH_4 oxidation in forest soil

Forest clear-cutting and thinning

The immediate effects of forest cutting system on CH_4 flux have been largely ignored. In order to realize the response of CH_4 uptake by forest soil to principal felling system, Bradford *et al.* (2000) investigated six sites at Grizedate Forest in UK. All soils displayed net CH_4 oxidation, meanwhile they found that the rate of CH_4 oxidation was significantly reduced ($p<0.05$) in the clear-cutting plots but significantly increased ($p<0.05$) in the thinning plots respectively after deforestation. Clear-cutting the *Picea abies* stand decreased the rate of CH_4 oxidation (about $1.8g \cdot m^{-2} \cdot a^{-1}$) because of the change of soil temperate (Kähkönen *et al.* 2002). The decrease in CH_4 uptake at clear-cutting sites was observed by Keller *et al.* (1986) too. The reason that results in decrease or increase may concern to changes of temperature and moisture in soils. However, some researchers considered that partial disturbance and erosion of the topsoil were the main reasons for the decrease (Kagotani *et al.* 2001). In their study, CH_4 absorption rates of soils in a deciduous broad-leaved secondary forest dominated by *Quercus serrata* in central Japan were measured by closed chamber technique. The highest mean absorption rate decreased to about 60%-70% of the last year's rate after clear-cutting.

In fact, results mentioned above were not contradictory. The reasons that lead to different conclusions were dis-

crepancies in experimental conditions. Therefore, further researches ought to focus on confirming main ingredients, which have the largest affect on CH_4 consumption.

Fertilization

Although fertilization practice is limited in forestry in a few developed countries, many studies on effects of fertilization (long-term or short-term) in the field on CH_4 consumption in forest soils were reported in recent years. Ojima et al. (1993) found that N additions to temperate forest soils in the northeastern United States decreased CH_4 uptake from 30 % to 60%. But to forest soils characterized by N limitation, a small-scale N fertilization experiment (less than 50kg·hm^{-2}·a^{-1} ($(NH_4)_2SO_4$) indicate that high N applications only resulted in a small reduction of CH_4 oxidation (less than 30%). The results indicated that the N limitation soils have the capacity to recover rapidly from the inhibitory effects of high inorganic N inputs (Steinkamp et al. 2001). A comparative study conducted by Rigler and Boltenstern (1999) showed that Ammonium-N [$(NH_4)_2SO_4$] inhibited CH_4 oxidation in the deciduous forest soil, but promoted it in the acidic spruce forest soil. Ammonium addition decreased the C/N ratio of the spruce forest soil, which was characterized by low pH but high humus content. Therefore, the general living conditions for microorganisms might have been improved. Conversely, NO_3^- inhibited hydrocarbon oxidation in both soils. It is obvious that the impact of nitrogen inputs on the CH_4 sink depends on its amount and as well as on soil type. Besides soil type, another influential factor is the amount of N additions. Medium and high N application (30 kg·hm^{-2}·a^{-1} and 90 kg·hm^{-2}·a^{-1}) resulted in a various degrees decrease of CH_4 uptake rate, the uptake rate was (85±3)% and (62±2)% of that in the control respectively (Sitaula et al. 1995).

Meanwhile many studies found that patterns of soil CH_4 consumption following NH_4^+-fertilization were multiple under different conditions. These patterns range from immediate (within hours or days) inhibition to delayed (months or years) inhibition to the absence of inhibition despite years of fertilization. Gulledge et al. (1997) explained this case by the occurrence of three physiologically distinct CH_4 oxidizer populations, and actual field inhibition dynamics may not always clearly fit one of these three patterns due to mixed CH_4 oxidizer communities, or other soil properties regulating exposure of CH_4 oxidizers to NH_4^+. Physical similarities between CH_4 and NH_4 permit both compounds to compete for enzymes: CH_4 and NH_4^+ monooxygenase, both enzymes were thought to be responsible for the first step of CH_4 oxidation in soil (Sitaula et al. 1995; Bedard et al. 1989), so that fortuitous NH_3 oxidation can competitively inhibit CH_4 oxidation (Dunfield et al. 1995; Smith et al. 2000). Another possible inhibition mechanism is toxicity of NO_2^- produced from NH_3 oxidation (King et al. 1994; Schell et al. 1994).

Exogenous aluminum salts and atmospheric acid deposition

A study made by Nanba and King (2000) in Maine forest showed that compared to deionized water controls, the CH_4 uptake rates were reduced by approximately 50% and 90% for exogenous aluminum salts addition of 1 to 8 μmol·g^{-1} (fresh weight soil) respectively. Tamai et al. (2003) proved that CH_4 uptake had a negative correlation with soil water-soluble aluminum (r=-0.63, p<0.001). Water-soluble aluminum may be a factor controlling CH_4 uptake. Aluminum chloride was more inhibitory than nitrate or sulfate salts, but its effect was comparable to that of a chelated aluminum. This inhibition could be explained in part by the lower soil pH value, which resulted from aluminum addition. However, aluminum will cause a significantly greater inhibition than mineral acids do at equivalent soil pH values. This indicated that the inhibition to CH_4 uptake also resulted from direct effects of aluminum essentially. Therefore, aluminum mobilization due to acid precipitation may exacerbate inhibition of atmospheric CH_4 consumption.

In recent decades, with the development of industry, atmospheric acid deposition became more severe. A study indicated that increasing rates of N deposition decrease the uptake rates of atmospheric CH_4 by the forest soils (Butterbach-Bahl 2002). The response of forest soil CH_4 oxidation to atmospheric acid deposition is strongly dependent on the form of acid deposition. The effects of NH_4^+, NO_3^-, SO_4^{2-} and H^+ on soil CH_4 flux were governed by the associated counter-anion or action of the investigated ions. The HNO_3 effect on CH_4 flux might be indirectly mediated through aluminum toxic. Meanwhile, sul phuric acid only inhibited CH_4 oxidation when added at pH 1. At concentrations of heavily polluted rainfall, H_2SO_4 had no effect on soil CH_4 flux or CO_2 production from soil cores, even after 210d of repeated addition. In contrast to HNO_3 additions, acidification of soil was not marked and was only significant for the mineral soil (Bradford et al. 2001b). Some people suggest that in the inhibition of CH_4 oxidation NO_3^- is more effective than NH_4^+ in forest soils (Wang et al. 2003).

Biocides

For controlling the forest disease and insect pest, many types of biocides were utilized in many forestry regions. Prieme and Ekelund (2001) investigated the effect of three fungicides Tilt 250EC, Tilt Top, and Corbel, an insecticide Dimethoat 40EC and an herbicide Tolkan on the atmospheric CH_4 by a pristine mineral forest soil in Danish. The results suggested that Dimethoat 40 EC and Tolkan might inhibit CH_4 oxidation at concentrations likely to be found in the soil where the pesticides were applied. Dimethoat 40EC, Tilt 250EC and Tolkan caused a similar or greater inhibition at 50-mg·L^{-1} AI (active ingredients) while one pesticide inhibited CH_4 oxidation at 5-mg·L^{-1} AI. This result is similar to the study of Topp (1993) made in agricultural soil. Thus, application of pesticides may be partly responsible for the lowed CH_4 oxidation rates in arable soils compared to for-

est soils. However, a number of frequently used pesticides in a sandy arable soil caused significantly reduced CH_4 oxidation compared to the control, under the same condition of CH_4 oxidation was observed, not even when the application rate of pesticides was ten-fold higher than usual (Boecks et al. 1998). Currently, there are few of studies on the long-term effects of pesticide application on CH_4 oxidation.

Switch of forest land-use

At present, there are sufficient evidences, which indicate the decrease of atmospheric CH_4 oxidation rate will happen consequentially while the forest is converted to cropland. CH_4 uptake rates were reduced about 60% because of the switch of forestland to farmland (Prieme et al. 1999; Dobbie et al. 1996b; Smith et al. 2000). It is pointed that the mechanisms responsible for the reduction is the changes in soil physical properties (including soil moisture content and structure), fertility (particularly N inputs) and changes in microbiological properties all contribute to it (Ojima et al. 1993).

In addition, mean rates of CH_4 consumption were 30% lower in urban than that of rural and suburban forest sites. Therefore, we have sufficient reasons to believe that factors associated with urbanization may decrease consumption rates of CH_4 in temperate forest soil (Goldman et al. 1995). Although low consumption rates of CH_4 in urban forest sites are a product of organic matter degradation and low rates of nutrient cycling caused by air pollution (especially ozone), main reasons of effects of land-use on CH_4 oxidation are the changes of both potential activities and their diversity of CH_4 oxidizing bacteria (Ready et al. 2001). On the contrary, CH_4 oxidation rates increased in changing land use from farmland to woodland (Ball 2002). In most cases, anthropogenic disturbances will decrease atmospheric CH_4 oxidation resulting in a positive impact on the elevated atmospheric CH_4.

Seasonal and spatial variation of CH_4 oxidation in forest soil

Soil temperature and moisture are the contributors for seasonal variations of CH_4 oxidation in forest soils. The CH_4 mixing ratio displayed a seasonal variation that was strongly related to soil temperature, with measured values roughly 30 ppb higher in the late summer than in spring (Simpson et al. 1999).

Atmospheric CH_4 oxidation activity in forest soil showed a distinct vertical stratification within the soil profile. Maximum CH_4 oxidation activity was localized in the uppermost mineral soil layer and markedly decreased with increasing soil depth (Steinkamp et al. 2001). Similar results were obtained in many studies (Klemedtsson et al. 1997). The activity of CH_4 oxidizing bacteria located (50%-90%) in the illuvial horizons in all seasons. In the upper 2-3 cm zone (the illuvial layer), the CH_4 oxidation rate was found 5-10 fold

higher than that in adjacent soil above or below (Kähkönen et al. 2002).

CH_4 uptake activity in Danish forest soil showed a maximum at the depth of 3-9 cm (Prieme et al. 1996), similar subsurface maxims have been observed in other forest soils (Schnell et al. 1994; Jensen et al. 2000). However, maximum $^{14}CH_4$ oxidation and ^{14}C assimilation, which was occurred at the A_2 horizon from 15 cm to 18 cm below the soil surface, were measured by radiotracer techniques in Western Jutland, Denmark (Roslev et al. 1997). The reason is that there exists a threshold whether low or high, this affects the CH_4 oxidation process in soil (Bender et al. 1993). Vertical profiles generally show a gradual decrease of CH_4 mixing ratios with soil depth (Born et al. 1990). This is another reason why atmospheric CH_4 oxidation changes with soil depth.

Suggestion

It is very important to assess the amount of atmospheric CH_4 uptake by forest soil and to evaluate the influential factors exactly in different areas, which is the base to forecast the trend of global warming and to provide some efficient approaches for enhancing the strength of CH_4 consumption in forest soil. In spite of this, however, due to the variety of forest types and site and its environment, our knowledge in atmospheric CH_4 oxidation (uptake) is still insufficient. We need more information about effects of natural and anthropogenic factors on atmospheric CH_4 consumption in forest soil to establish a forecasting system for atmospheric CH_4 sinks strength. Although many researches were made in various aspects, systematic and integrated knowledge is needed in this field. Certainly, accurate prediction of future trends of CH_4 oxidation in forest soil under the condition of climate and land use changes requires an improved understanding of the physiology and controls of this microbial process.

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